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RESEARCH ARTICLE

Genetic and functional leaf trait diversity throughout the distribution of two Cerrado tree species: Testing the centre-periphery hypothesis

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Abstract

Aim: The centre-periphery hypothesis (CPH) states that peripheral populations exhibit lower genetic diversity, abundance and size, and higher differentiation compared to central populations, due to a decline in environmental suitability towards range margins. Here, we tested if neutral genetic diversity and functional leaf trait diversity fit the predicted patterns of the CPH.

Location: Cerrado, Brazil.

Taxon: *Qualea grandiflora* (Vochysiaceae) and *Annona crassiflora* (Annonaceae).

Methods: Variation in eight functional leaf traits and nine or eight microsatellite loci were analysed in 37 populations (777 individuals) of *Q. grandiflora* and 21 populations (397 individuals) of *A. crassiflora*. We tested CPH using three distinct centres of species' range: geographical (centre of species' geographic occurrence), historical (centre of species' refugia) and ecological (centre of species' current suitability areas). Generalised linear regressions were performed between genetic diversity and differentiation, coefficients of variation and means of leaf metamer traits of populations and their distances from each centre.

Results: A decrease in allele richness was observed from central towards peripheral populations for ecological (both species) and geographical centres (*Q. grandiflora*). Overall, the results for both species pointed to a decrease in metamer vigour towards marginal populations, pattern consistent with a decrease in environmental suitability towards periphery as predicted by CPH. Besides geographical and ecological centres, leaf traits fitted CPH considering historical centre.

Main Conclusions: Results for leaf traits and genetic diversity of two phylogenetically distant species indicate the consistency of the CPH for Cerrado species. Our results highlight the importance of considering distinct centres and a great number of populations along species' range to better determinate the processes underlying the distribution of genetic diversity and functional traits. The low genetic diversity and metamer vigour in marginal populations can explain the Cerrado endemism of studied species and suggest that the ongoing climatic changes can be critical for their survival.

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KEYWORDS
Annona crassiflora, centre-periphery hypothesis, Cerrado, climatic changes, endemism, functional leaf traits, genetic diversity, marginal populations, metamer vigour, *Qualea grandiflora*

1 | INTRODUCTION

The distribution range of a species is influenced by many geographical, ecological and genetic processes that can change through species' evolutionary history (Duncan et al., 2015). Disentangling these processes can help to predict species potential responses to ongoing environmental changes and their past range shifts (Davis & Shaw, 2001; Parmesan & Yohe, 2003). There are many hypotheses to explain the variation of populations performances across a species' range, and they arise from many different areas as ecology, evolutionary biology, biogeography and macroecology (Duncan et al., 2015; Lira-Noriega & Manthey, 2014; Sexton et al., 2009; Stanton-Geddes et al., 2013). One of the most propagated hypotheses though is the centre-periphery hypothesis (CPH), also known as the centre-marginal hypothesis (Eckert et al., 2008), or the abundant centre hypothesis (Pironon et al., 2017; Sagarin & Gaines, 2002). The CPH states that the diversity and abundance of a species decreases as the distance from the centre of the species' range increases. Alternatively, local adaptations may arise in populations at the periphery of the species distribution, which may lead to disruption of the CPH.

The CPH usually considers the existence of two main types of periphery for the species' range: the ecological and the geographical periphery (Soulé, 1973). In the first one, the distribution range of a species is a representation of its ecological niche (Hutchinson, 1957), with populations located at the centre of species range experiencing the most favourable biotic and abiotic conditions (Brown, 1984). Due to less abiotic stress and higher resource availability, it is expected that these populations exhibit higher abundance and stability than those far from the optimum conditions (Lira-Noriega & Manthey, 2014; VanDerWal et al., 2009). On the other hand, populations located at the range margin experience harsher ecological conditions with limited resources and/or interactions with new competitors, pathogens or parasites, which can lead to declines in population density and fitness (Brown, 1984; Brown et al., 1995; Duncan et al., 2015; Hengeveld & Haeck, 1982). The geographical marginality considers the geographic position of a population according to the species natural distribution range. It is expected that species achieve highest abundance at the geographical centre of the range, with populations becoming smaller and more spatially isolated towards the range limits. A third marginality that can also be considered but is often neglected is the historical marginality. The historical marginality refers to ecological marginality taking into consideration the changes in suitable areas for the species over time. According to the historical marginality, populations located on areas that remained climatically stable over the years, especially during Quaternary oscillations, would present the highest effective size and diversity. Conversely, rapid cycles of extinction and recolonization in peripheral populations would lead to a reduction in diversity (Eckert et al., 2008; Pironon et al., 2017).

Regardless of the marginality type considered, CPH predicts that due to harsher environmental conditions, populations located at the peripheries are often fragmented, less abundant, show small population sizes (Hampe & Petit, 2005; Sagarin & Gaines, 2002) and have reduced gene flow among each other because of increased spatial isolation (Kimura & Weiss, 1964). Peripheral populations are also more vulnerable to founder events or severe population bottlenecks due to expansions and contractions at species' range edges, and those stochastic events can intensify the decrease of genetic diversity and increase of genetic differentiation among populations (Hampe & Petit, 2005; Hewitt, 1996). Additionally, the lack of genetic diversity coupled with small population sizes can lead to an extinction of those populations as a result of inbreeding depression events (Gilping & Soule, 1986).

The difference in environmental conditions at the margins and centre of species distribution, however, can also lead to distinct outcomes that contradict the CPH depending on the connectivity among central and marginal populations (Bridle & Vines, 2007, Hoffmann & Blows, 1994). For example, if gene flow from central to marginal populations is limited but not restricted, an increased selective pressure at the margins can result in the selection of individuals that are adapted to the local conditions at the periphery, increasing species adaptive potential (Levin, 1993). This can also occur if peripheral populations maintain substantial genetic variation even without a connection with the central populations (Channell & Lomolino, 2000). On both cases, gene flow might bring genetic variation to depauperate marginal populations, acting as a rescue effect (Pironon et al., 2017). In case genetic connectivity between central and marginal populations remain, it is possible that a random dispersal of gametes moving from the large and diverse central populations towards the small and sparse populations at the range margin would limit the evolutionary potential of the marginal populations. This would make the adaptation of the species to new or local environmental conditions to be unlikely (Blows & Hoffmann, 2005; Gaston, 2009; Hoffman & Blows, 1994; Hoffmann & Parsons, 1997). Moreover, the asymmetric gene flow can carry maladapted alleles from central towards peripheral populations diminishing their mean fitness and potentially leading to population extinction (Barton, 2001; Bridle & Vines, 2007; Kirkpatrick & Barton, 1997). In this way, the genetic diversity of the species is shaped by both contemporary factors and historical events, and depending on species history and the existence or inexistence of dispersal barriers, geographical, ecological and historical peripheries can coincide and/or overlap (Hampe & Petit, 2005; Lesica & Allendorf, 1995).

The CPH was first created focusing on species abundance and population genetic structure (Brown, 1984; Carson, 1959; Hengeveld & Haeck, 1982). Not surprisingly, a study that analysed CPH papers from 1968 to 2014 showed that genetic variation was the most studied category followed by abundance and population performance (Pironon et al., 2017). Over the years, studies analysing other components as fitness, demography and functional traits (Kennedy et al., 2020; Pfeifer et al., 2009; Samis & Eckert, 2007; Wagner et al., 2011) were included in the CPH paradigm but are still poorly investigated. Functional traits are morphological, physiological or phenological characteristics, which directly affect plant growth and therefore can influence species establishment, survival and fitness (Osnas et al., 2018; Pérez-Harguindeguy et al., 2013). Relationships between genetic diversity within populations and fitness or life history traits (e.g., plant height, number of flowers, seeds dispersion and weight) have been described (Leimu et al., 2006; Reed & Frankham, 2003; Reisch & Bernhardt-Römermann, 2014). Likewise, positive correlations were found between genetic diversity and the phenotypic variation (Karbstein et al., 2020; Waitt & Levin, 1998). Because of the positive correlation between genetic and phenotypic diversity, similar patterns of diversity as predicted for genetic diversity are expected for functional trait variation under CPH. We expect peripheral populations to exhibit a low variation in functional traits due to strong selection, small population sizes and population isolation. In contrast, gene flow from central to climatically unstable peripheral populations would increase genetic variation (Hoffmann & Blows, 1994) and thereafter phenotypic variation in these populations.

Genetic diversity, however, does not necessarily translate into adaptive diversity of ecological significance or in ecologically relevant trait variation (Abeli et al., 2014; Gaston, 2009; Kawecki, 2008; Pironon et al., 2017), especially if using genetic markers that are adaptively neutral. Phenotypic differences between populations can be a result of neutral, adaptive and/or plastic processes (Kawecki & Ebert, 2004). A large phenotypic plasticity of traits for example can enable individuals to inhabit different environmental niches (e.g., Ghalambor et al., 2007), and if the trait variation is due mainly to phenotypic plasticity, a correlation between genetic diversity and phenotypic variation may not be observed. Regardless of the causes of phenotypic variation, leaf functional traits have been linked to plant vital processes and adaptation to local conditions, including stressful environments. Leaf area (LA) and the ratio between LA and leaf mass (specific leaf area [SLA]), for example, are related to the carbon uptake in photosynthesis, tolerance to water stress (Ackerly et al., 2000; Poorter, 2009; Wright et al., 2017) stomatal conductance (Bruschi et al., 2003; González-Rodríguez & Oyama, 2005; Uribe-Salas et al., 2008) and resilience to extreme temperatures (Dong et al., 2020). Ratios between length and mass of both petiole and internode are related to spatial positioning, biomechanics and hydraulic support of the leaf sheet (Santiago et al., 2004) and vary according to climatic conditions (Poorter, 2009; Souza et al., 2018). Under the CPH, due to more favourable climatic and ecological conditions in the centre of species' range, we would expect a greater leaf expansion in individuals located in central populations with greater leaf sizes, mass and length when compared to peripheral individuals. On the other hand, peripheral individuals would present greater petiole and internode mass in relation to total metamer mass (MM) due to hydraulic limitation.

Over the years, studies have tested the CPH premisses using distinct species, even though many of them were not directly addressing the hypothesis. Mixed results were obtained depending on the species, type of marginality and parameters used in the analyses (Abeli et al., 2014; Eckert et al., 2008; Lira-Noriega & Manthey, 2014; Sagarin & Gaines, 2002). However, a general trend for lower genetic diversity within populations and higher differentiation among populations in the periphery was observed for plant species (Pironon et al., 2017). A lack of agreement among studies could be attributed to factors as confounding effects of latitude, difficulties in differentiating core and marginal populations or even differences in species life history (Araújo et al., 2011; Guo, 2012; Sagarin et al., 2006; Santini et al., 2019). Studies have also examined the validity of CPH in distinct biomes (see Abeli et al., 2014; Eckert et al., 2008; Lira-Noriega & Manthey, 2014; Pironon et al., 2017; Sexton et al., 2009), but the processes that drive species' range distribution in neotropical biomes are still poorly known.

The Cerrado is the second largest neotropical biome, mostly occupying central Brazil (covering an extent of approximately two million square kilometres) and areas in Bolivia and Paraguay (Eiten, 1972). It is mainly composed of savanna vegetation with phytophysiognomies varying from fields to high forest formations (Durigan & Ratter, 2016). The biome is considered the world's richest biodiversity savanna but has been strongly threatened by anthropic activities (Myers et al., 2000). Studies investigating the Cerrado flora have found relationships between diversity and distribution of species and environmental conditions (as climate and soil) (Assis et al., 2011; Bueno et al., 2018; Ratter et al., 2003). Environmental drivers of the geographical distribution of intraspecific functional traits and genetic neutral markers diversity in Cerrado have also been studied in some species (Buzatti et al., 2019; Ribeiro, Souza et al. 2016; Souza et al., 2019). In addition, phylogeographical studies have shown that Quaternary climatic changes have influenced the genetic diversity and structure of Cerrado plant species, with higher genetic diversity in climatically stable areas, known as refugia (Buzatti et al., 2017, 2018; Collevatti et al., 2013, 2014; Ribeiro, Lemos-Filho, Buzatti, Lovato & Heuertz, 2016; Souza et al., 2017). The phylogeographical studies that point to higher genetic diversity in the refuges, most of which are located in central Cerrado, suggest that CPH could be validated for genetic data but deserve to be investigated in relation to functional traits. To our knowledge, only few studies have explicitly tested the CPH in Cerrado. Diniz et al., (2009) evaluated the changes in species endemism from the centre towards the periphery of Cerrado, and Vidal et al., (2019) evaluated genetic diversity in a tree species, *Caryocar brasiliensis*. None of these, however, have investigated CPH using parameters of genetic diversity in conjunction with functional traits in Cerrado plants.

Here, we studied two phylogenetically distant tree species that are endemic and widely distributed in the Cerrado, *Annona crassiflora*

Mart. (Annonaceae) and *Qualea grandiflora* Mart. (Vochysiaceae), to test if they fit the predicted patterns of the CPH for genetic data and functional leaf traits. The species undergo very different environmental conditions across their range and thus constitute excellent material for explicitly testing the CPH. We determined three distinct centres of species' range: geographical (i.e., centre of species' geographic occurrence), historical (i.e., centre of species' refugee areas) and the ecological (i.e., centre of species' suitability areas) centres. This approach allowed the investigation of the relative contribution of geography, ecology and history on genetic and functional leaf trait diversity patterns along species' ranges. Here, we aimed to answer the following questions: (1) Are the ecological, historical and geographical centres of the species spatially coincident? (2) Do species show centre-periphery patterns of genetic and functional leaf trait diversity? (3) Are those patterns similarly influenced by geography, ecology, or history? (4) Do functional leaf traits exhibit changes that are consistent with less favourable environmental conditions towards species' range periphery as hypothesized by the CPH?

2 | MATERIALS AND METHODS

2.1 | Species and area of study

In this work, we studied two of the most common and endemic Cerrado species, *Q. grandiflora* Mart. (Vochysiaceae) and *A. crassiflora* Mart. (Annonaceae). *Qualea grandiflora* is the most widely distributed woody species in the Cerrado (Ratter et al., 2003) and is adapted to rich aluminium soils (Haridasan & Araújo, 1988). The species is diploid (2*n* = 22; Yamagishi-Costa et al., 2018), deciduous and has arboreal-shrub size (2–6 m height). It has yellow petal flowers pollinated by Sphingidae hawk moths (Silberbauer-Gottsberger & Gottsberger, 1975) and fruits with numerous seeds dispersed by wind (Shimizu, 2009). *Annona crassiflora* is among the 20 most consumed fruit tree species in Central Brazil (Arruda et al., 2015). The species can reach 4–8 m height and presents white flowers pollinated mainly by the beetle *Cyclocephala atricapilla* (Gottsberger, 1999). Its fleshy fruits and numerous seeds are dispersed by distinct mammals, like wolves (*Chrysocyon brachiurus*), foxes (*Cerdocyonthous*) and tapirs (*Tapirus terrestris*) (Donatti et al., 2007).

We sampled 37 populations (777 individuals) of *Q. grandiflora* across the Cerrado biome: 18 for both genetic and functional leaf traits data, two for only genetic data and 17 for leaf traits data only (Figure S1). The species was sampled across its distribution range, ranging from latitudes 7°19′40″S to 24°10′41″S and from longitudes 60°24′31″W to 41°51′23″W. Pairwise distances among sampled populations ranged from approximately 128 to 2,067 km. For *A. crassiflora*, we sampled 21 populations with 412 individuals in total: 20 populations for both genetic and leaf traits data (Figure S1) and a single population for genetic data only. Populations ranged from latitudes 12°05′46″S to 24°10′41″S and longitudes 52°03′55″W to 44°23′37″W with pairwise distances among them ranging from approximately 70.8 to 1,016 km.

2.2 | Genetic and functional leaf traits data

To calculate genetic diversity and divergence indexes for each population, we used information of individual genotypes obtained from nine microsatellites markers of *Q. grandiflora* deposited in Figshare at https://doi.org/10.6084/m9.figshare.11106881.v2 and from eight markers of *A. crassiflora* available at Dryad at https://doi.org/10.5061/dryad.n7dv6. For complete information about DNA extraction and amplification, and genotyping methods, please refer Buzatti et al., (2019) and Ribeiro, Souza, et al., (2016).

To test for genetic patterns across species' range, we used two distinct diversity indexes estimated by Buzatti et al., (2019) and Ribeiro, Souza, et al., (2016): expected heterozygosity (H_E) and allele richness (A_R) estimated using a rarefaction method to correct for disparities among sample sizes. These indexes were estimated in ARLEQUIN version 3.5.1.2 (Excoffier & Lischer, 2010). The H_E is also known as gene diversity and accounts for both number and evenness of the alleles (Nei, 1973). It is usually a more reliable parameter to measure genetic diversity when compared to the observed heterozygosity (H_O) once it is not influenced by the mating system. The A_R is a traditional key measurement for conservation and management of populations as well a strong indicator for the evolutionary potential of a population. In contrast to the number of alleles (N_A), A_R considers the sampling size, which is an important step as rare alleles are not prone to appear in small sample sizes.

We also estimated three distinct parameters of genetic differentiation: F_{ST}, which primarily reflects the degree of completion of the alleles fixation process and is also known as the 'fixation index' (Weir & Cockerham, 1984); R_{ST}, which is similar to F_{ST} but also accounts the number of repetitions of the allele (usually used for microsatellites studies), and finally the D_{EST}, which is considered a better measure of allelic differentiation for markers with high degree of intrapopulation diversity as microsatellites (Jost, 2008; Jost et al., 2018). The parameters were first calculated with pairwise comparisons among populations and then an average value for each population of each species was obtained. Both pairwise F_{ST} and R_{ST} were calculated using the software ARLEQUIN 3.5.1.2, while pairwise D_{EST} was estimated using GeneAlEx 6.5 (Peakall & Smouse, 2012), all of them with 10,000 randomizations.

To evaluate functional leaf trait variation patterns, we sampled leaf metamers (leaf lamina, petiole and internode) from the second node of distal branches of different parts of the crown. For *A. crassiflora* five or one metamer per tree were collected, while for *Q. grandiflora*, three or one leaf metamers were sampled. All samples were collected in the rainy season. Once collected, metamers were photographed with a millimetre scale in the field for subsequent measurements in the laboratory, using the software ImageJ (Schneider et al., 2012). All samples were put in paper bags and dried in an oven at 70°C for 72 h for determination of dry mass of each part of the metamer separately (leaf mass, petiole mass, and internode mass; all in grams). From these data, we evaluated eight functional leaf metamer traits for *Q. grandiflora* and *A. crassiflora*: LA (in cm^2), leaf length/leaf width (LLW), leaf fluctuating asymmetry (LFA; [leaf left-side width − leaf right-side width]/total

leaf width), SLA (LA per unit dry mass, in cm^2/g), MM, petiole mass ratio (PMR; petiole mass/MM), leaf mass ratio (LMR; leaf mass/MM) and internode mass ratio (IMR; internode mass/MM) (see Figure S3 for a picture of species leaf metamer and a diagram of morphological measurements). We calculated an average value per leaf trait for each of the 397 individuals for *A. crassiflora* and 745 individuals for *Q. grandiflora* and then calculated the mean values per population. As a measure of intrapopulation variation of the traits, we also calculated the coefficient of variation (CV = standard deviation/mean ⁎100) per trait (with the exception of LFA which is a measurement of variation itself) for each of the 20 populations of *A. crassiflora* and 35 populations of *Q. grandiflora*.

2.3 | Ecological and historical centres: estimates based on niche modelling and climatically stable areas

To estimate the ecological centre of *A. crassiflora*, we first performed an ecological niche modelling (ENM), using Maxent 3.4.1 (Phillips et al., 2017). To build the models, 379 occurrence records were obtained from the NeoTropTree database (Oliveira-Filho, 2017), and 19 climate variables were extracted from WorldClim database (Hijmans et al., 2005) for all geographical coordinates at a spatial resolution of 1 km. Strongly correlated variables ($r > 0.9$) were then eliminated to avoid overparameterization of the modelling (Bueno et al., 2017; Dormann et al., 2013). To cross-validate the ENM, we split the data into a training set (75% of occurrences) and a validation set (25% of occurrences). The models were constructed 10 times, and the average output data was used in the downstream analyses. Next, we used the 'minimum training presence' method to determine the threshold value at which grid cells would be considered as having suitable environmental conditions for maintaining viable populations of the species (Pearson, 2006). The method assumes that to be considered suitable for the species, the grid cell should have at least the same suitability as those where the species has been truly observed (Pearson, 2006). To validate the produced models, we used the area under curve (AUC) as a threshold-independent measure and the true skill statistic (TSS) as threshold-dependent accuracy measures (Allouche et al., 2006; Liu et al., 2009).

After performing the ENM for *A. crassiflora*, we also obtained the current environmental suitability map for *Q. grandiflora* from Buzatti et al., (2018), where the same methodology described here was used to build the map. The ecological centroids for each species were then calculated as an average of latitude and longitude values of each pixel in the current environmental suitability map weighted by its suitability value in current time.

To investigate the influence of late Quaternary climatic changes on species distribution, we projected species occurrence suitability in the current (0 ka; pre-industrial; obtained with ENM), Last Glacial Maximum (LGM; 21 ka), and Last Interglacial (LIG; 130 ka) time periods. The paleoclimatic data was obtained through simulations using Global Climate Models (GCMs) based on the Coupled Model Intercomparison Project Phase 5 (CMIP5; Taylor et al., 2012). To estimate species suitability during the LGM we used Community Climate System Model, CCSM4 (Gent et al., 2011), while for the model during the LIG, we used the approach described by Otto-Bliesner et al., (2006). All the geographic information system (GIS) analyses were performed using ArcGIS 10 (ESRI, 2011). The potential areas of climate stability throughout the Quaternary period for *A. crassiflora* were predicted by setting the lowest presence threshold for each model and therefore converting the continuous outputs into presence–absence maps. The presence–absence maps were then summed, generating a map of historical stability areas, also called refuges. The refuges are areas that remained climatically stable during the climatic oscillations in the Quaternary and therefore were potentially occupied by the species. These historically stable areas were defined as the grid cells in which the presence of the species was inferred in projections at all the times. This protocol is similar to others used in recent Neotropical biomes studies (Bueno et al., 2017; Bünger et al., 2016; Buzatti et al., 2018; Werneck et al., 2012) and maximizes the conformity between modelled and observed distributions (Pearson, 2006).

We estimated the historical centroid for each species by calculating the centre point of the stable areas obtained for each one of the species. Calculations were performed with the Mean Center tool of ArcGis (ESRI, 2011) and considered both disjoint and large refugia. The refugia projected for *Q. grandiflora* was obtained from (Buzatti et al., 2018) where the same methodology as described above was used.

2.4 | Geographical centre: Current distribution based on sampling records

Occurrence records of each species were obtained from the NeoTropTree database (Oliveira-Filho, 2017). They were plotted on a map and a polygon containing the most species occurrences was manually drawn (Figure S2) on ArcGis (ESRI, 2011). Finally, the centroid of each polygon was calculated with Mean Center tool of ArcGis (ESRI, 2011) as the respective geographical centre for the species.

2.5 | Tests of CPH

To test if populations located in the central areas exhibit higher genetic and morphological diversity and lower genetic divergence as expected by the CPH, we performed generalized regression models using the genetic variation indexes (H_E and A_R), functional leaf trait variation (coefficients of variation of LA, LLW, SLA, MM, PMR, LMR and IMR), and genetic distance parameters (average values of F_{ST}, R_{ST} and D_{EST} for each population) as the response variables, and the distances from the three different centroids (geographical, ecological and historical) as explanatory variables.

Additionally, to test for effects of putative decrease in environment suitability from centre towards the periphery, we performed generalized linear models between population' leaf trait means

(response variables) and the population distances from the centres (explanatory variables).

All the linear regressions were performed using the *glm* function of the 'stats' package in the R version 4.0.2 (R Core Team, 2019). After performing the regressions for each response and the explanatory variable separately, the normality of the residuals was checked on the Q-Q Plot generated by the *glm* function and confirmed using a Shapiro–Wilk normality test with the 'stats' function *shapiro.test* (Royston, 1982). When the modelling residuals were not normally distributed, the error distribution and link function used in the model were modified based on the response data distribution. Considering that both genetic and leaf trait data were continuously distributed, we tested the inverse Gaussian and gamma distributions. As a last resource, to obtain a normally distributed error, a Box–Cox transformation on the response variable was performed using the *BoxCox* function of 'car' package in R (Fox & Weisberg, 2019; R Core Team, 2020). Since all the significant results were obtained using a Gaussian family for the distribution of the errors, r^2 values were obtained using the formula (1-model deviance/null deviance) as utilized in linear regression models.

3 | RESULTS

3.1 | Genetic differentiation among populations

Genetic differentiation among populations of *Q. grandiflora* was lower than among populations of *A. crassiflora* for all the three estimated indexes. The average pairwise F_{ST} showed the lowest values for almost all the populations in both species, varying from 0.051 to 0.123 in *Q. grandiflora* and from 0.137 to 0.295 in *A. crassiflora* (Table 1). The mean pairwise D_{EST} values on its turn showed the highest values of the three indexes, ranging from 0.207 to 0.395 and 0.233 to 0.469 in *Q. grandiflora* and *A. crassiflora*, respectively (Table 1).

3.2 | ENM for A. crassiflora

The ENM predicted areas of high suitability for *A. crassiflora* during all the Quaternary (Figure 1). During LIG, we observed the maximum of species distribution range in southern Brazil. Additionally, the model suggests an existence of small disjoint areas with high environmental suitability on the north of the Cerrado biome and at the Brazil–Bolivia boundary. During this same period, a low suitability area is observed in the centre of Cerrado resulting in a nearly eastern–western split in species distribution. However, this area is significantly reduced and shifted to the west at the LGM period (Figure 1). During the LGM, species distribution range retracted in the south and expanded towards west and north, incorporating areas that were disjoint during LIG. At the current time, there is a substantial contraction of suitability areas at western Cerrado and a recovery of southern areas that were lost during the LGM (Figure 1). The map displaying modelled stable areas points to an existence of a large refuge in the centre region of Cerrado, a medium-size area on the western and small disjoint area northeastern of the main refuge (Figure 1).

3.3 | Geographical, ecological and historical centres

The three centres (i.e., geographical, ecological and historical) were situated in central Cerrado in the state of Goiás and were not spatially coincident in either species, with distances of about 200 km between them (Figures 2 and 3). For both species, the ecological centre was westernmost, the historical centre was easternmost, and the geographical centre was located at an intermediate position. Geographical centres were located approximately in the same area for the two species, coinciding with the centre of the Cerrado. Ecological centres were located at slightly different areas for each species, as well as the historical centres (Figures 2 and 3).

3.4 | Tests of CPH for genetic data

The results of generalised linear regressions showed that the allele richness (A_R) was associated with population distances from ecological centres in both *Q. grandiflora* and *A. crassiflora* (r^2 = 0.293, p = 0.014 and r^2 = 0.215, p = 0.034, respectively), with marginal populations showing lower allele richness than central populations (Figures 2 and 3). For *Q. grandiflora*, a significant correlation between A_R and distances from geographical centre was also found (r^2 = 0.206, p = 0.044), with a decrease of A_R as the distance from centre increased (Figure 2). The other diversity index, H_E, was not associated with distances from the centres in any of the two species (p > 0.05). The mean genetic differentiation of populations exhibited associations as expected under the CPH only for *Q. grandiflora*, in which the mean F_{ST} increased with the increment of distances from the geographical (r^2 = 0.217, p = 0.039; Figure 2) and historical (r^2 = 0.199, p = 0.048; Figure 2) centres.

3.5 | Tests of CPH for functional leaf traits

The intrapopulation diversity for leaf traits (coefficients of variation) in *Q. grandiflora* showed significant association as expected under CPH for only one out of eight evaluated traits. MM values showed significant association (r^2 = 0.135, p = 0.030) with distances from historical centre, with intrapopulation diversity decreasing with the increase of distance from the centre (Figure 2). Leaf trait diversity was not associated with distances from any of the other two centres for *Q. grandiflora* (p > 0.05).

Annona crassiflora showed significant associations between LLW and IMR and distances from centres. The intrapopulation diversity of LLW was explained by distances from the three distinct centres: ecological (r^2 = 0.234, p = 0.031), geographical (r^2 = 0.383, p = 0.004) and historical (r^2 = 0.373, p = 0.004), with diversity decreasing as

TABLE 1 Results of mean pairwise genetic differentiation for each population of *Qualea grandiflora* and *Annona crassiflora*

Qualea grandiflora				*Annona crassiflora*			
Population	F_{ST} (mean)	R_{ST} (mean)	D_{EST} (mean)	Population	F_{ST} (mean)	R_{ST} (mean)	D_{EST} (mean)
AGN	0.108	0.181	0.366	APG	0.243	0.216	0.439
ANA	0.110	0.192	0.331	ARN	0.201	0.356	0.297
APG	0.079	0.126	0.296	CAL	0.279	0.258	0.429
CAL	0.059	0.112	0.235	CAV	0.154	0.359	0.281
CQG	0.095	0.185	0.395	COC	0.190	0.287	0.276
CHG	0.064	0.096	0.242	COR	0.147	0.163	0.302
COC	0.051	0.074	0.207	DES	0.201	0.330	0.258
COR	0.078	0.289	0.348	FOR	0.224	0.491	0.320
FUR	0.061	0.085	0.225	JAG	0.295	0.407	0.389
GMG	0.087	0.146	0.320	JAN	0.148	0.219	0.233
JAG	0.080	0.135	0.295	JEQ	0.137	0.186	0.260
JPO	0.057	0.103	0.216	LEM	0.166	0.377	0.250
MTP	0.082	0.136	0.294	MTP	0.210	0.228	0.315
NJA	0.101	0.193	0.330	NPO	0.193	0.224	0.352
NXA	0.090	0.203	0.314	PAL	0.217	0.339	0.354
PIR	0.078	0.128	0.337	PPB	0.179	0.202	0.300
RCO	0.123	0.162	0.386	SBA	0.161	0.243	0.261
SEL	0.083	0.145	0.269	SEL	0.158	0.250	0.255
SER	0.069	0.145	0.233	SER	0.162	0.247	0.365
VHA	0.114	0.135	0.392	SJB	0.282	0.268	0.469
				SRQ	0.196	0.259	0.371
Total mean	0.084	0.149	0.301		0.197	0.281	0.323

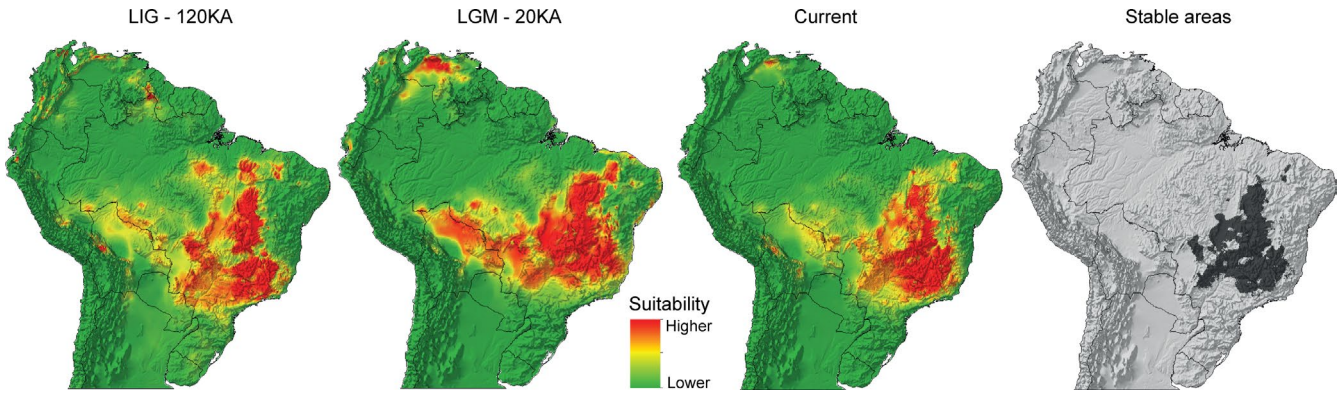

FIGURE 1 Ecological niche modelling (ENM) for *Annona crassiflora*. Panels represent the predicted suitability areas for the species occurrence across Brazil in the Last Interglacial (LIG; 120 ka), Last Glacial Maximum (LGM; 20 ka) and under current climatic conditions (0 ka; pre-industrial). Dark grey areas in the last panel represent the areas that remained suitable for the species occurrence throughout this period (120 ka to current)

distance from centres increased (Figure 3). The IMR intrapopulation diversity was also negatively associated with distances from geographical (r^2 = 0.269, p = 0.019) and historical centres (r^2 = 0.274, p = 0.018), with lower diversity in peripheral populations (Figure 3).

In *Q. grandiflora*, intrapopulation means of four out of eight functional traits were associated with distances from the centres (Figure 4). LA was negatively correlated with distances from both ecological (r^2 = 0.176, p = 0.012) and geographical centroids (r^2 = 0.149, p = 0.022). In the same way, populations located closer to the centroids showed higher MM than populations located closer to the periphery in relation to geographic (r^2 = 0.290, p = 0.001) and ecological centres (r^2 = 0.259, p = 0.002; Figure 4). A negative correlation was also observed for LMR with distances from the historical centroid (r^2 = 0.113, p = 0.049). In contrast, LLW increased towards the periphery when considering geographical (r^2 = 0.182, p = 0.011) and historical (r^2 = 0.320, p < 0.001) centroids (Figure 4).

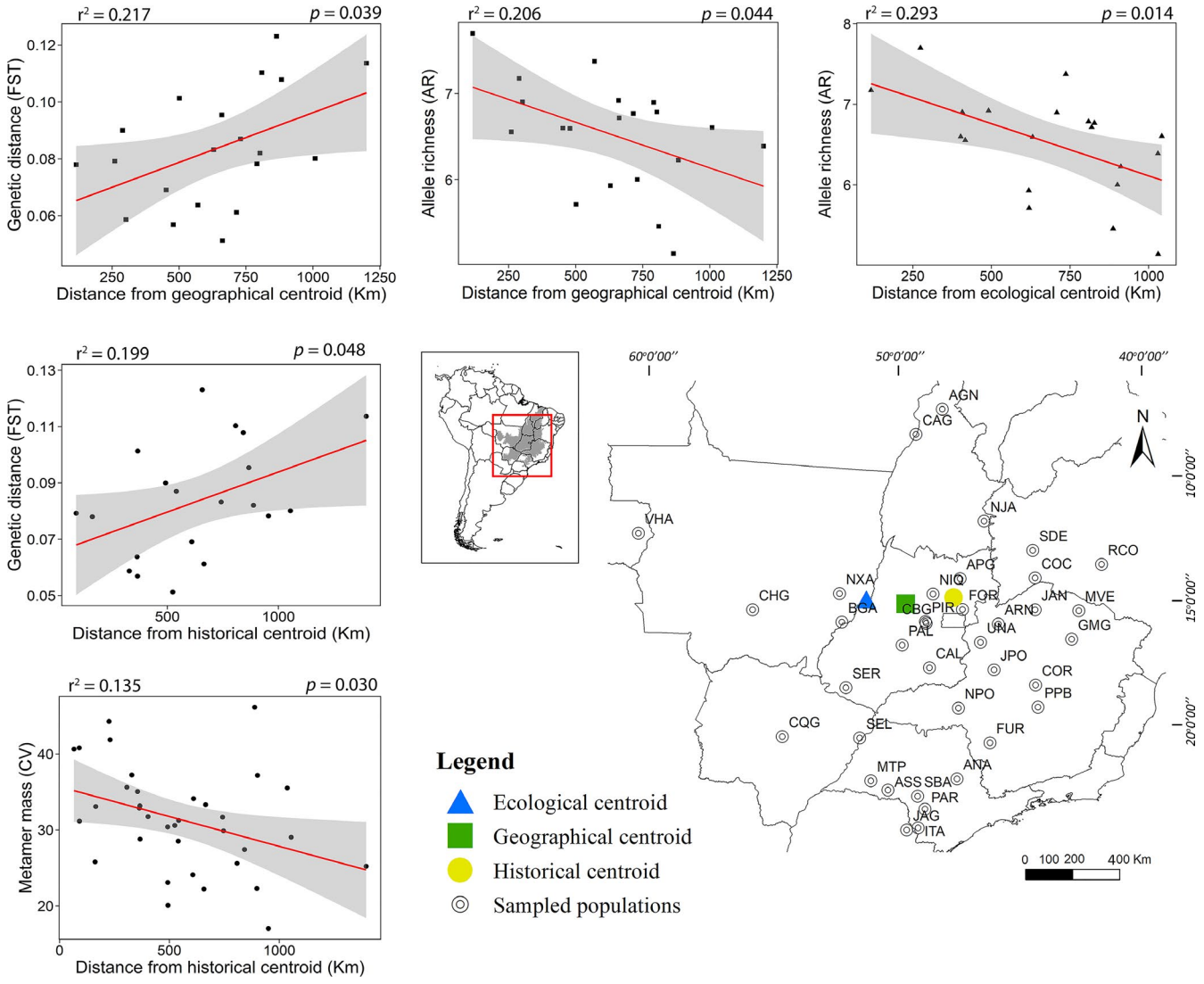

FIGURE 2 Results of significant generalised linear regressions between population genetic and functional trait diversity and population distance from historical, ecological and geographical centres for *Qualea grandiflora*. r^2 and *p* values for each linear regression are indicated at the top left and right of each graph, respectively. Symbols on the map represent the estimated location of the ecological (triangle), geographical (square) and historical (circle) centroids for the species, and the populations that were sampled for this study (double circle). The grey shade in the South America map represents the Cerrado distribution in Brazil

Annona crassiflora showed association between intrapopulation means of two traits with distances from the centres (Figure 5). The mean of MM of populations reduced with an increase of the population distance from the ecological (r^2 = 0.316, *p* = 0.010) and geographical (r^2 = 0.203, *p* = 0.046) centroids (Figure 5). On the other hand, the mean of SLA of populations increased with the increase of distances from ecological (r^2 = 0.381, *p* = 0.004), geographical (r^2 = 0.404, *p* = 0.003) and historical centres (r^2 = 0.398, *p* = 0.003) (Figure 5).

4 | DISCUSSION

Consistent with the CPH, we observed a decrease in genetic diversity from central towards peripheral populations when considering the ecological centres in both species *Q. grandiflora* and *A. crassiflora*, and also when considering the geographical centre of *Q. grandiflora*. We also found changes in direction to lower metamer vigour towards the periphery of the distribution range of the two species using distinct functional leaf traits, a pattern consistent with a decrease of environmental suitability in marginal populations as predicted by CPH.

4.1 | Niche modelling and species centres

The prediction of the current distribution of *A. crassiflora* using ENM shows the central Cerrado area as having the highest suitability for the species' occurrence. Similar results are observed for other Cerrado species (Buzatti et al., 2017, 2018) suggesting that

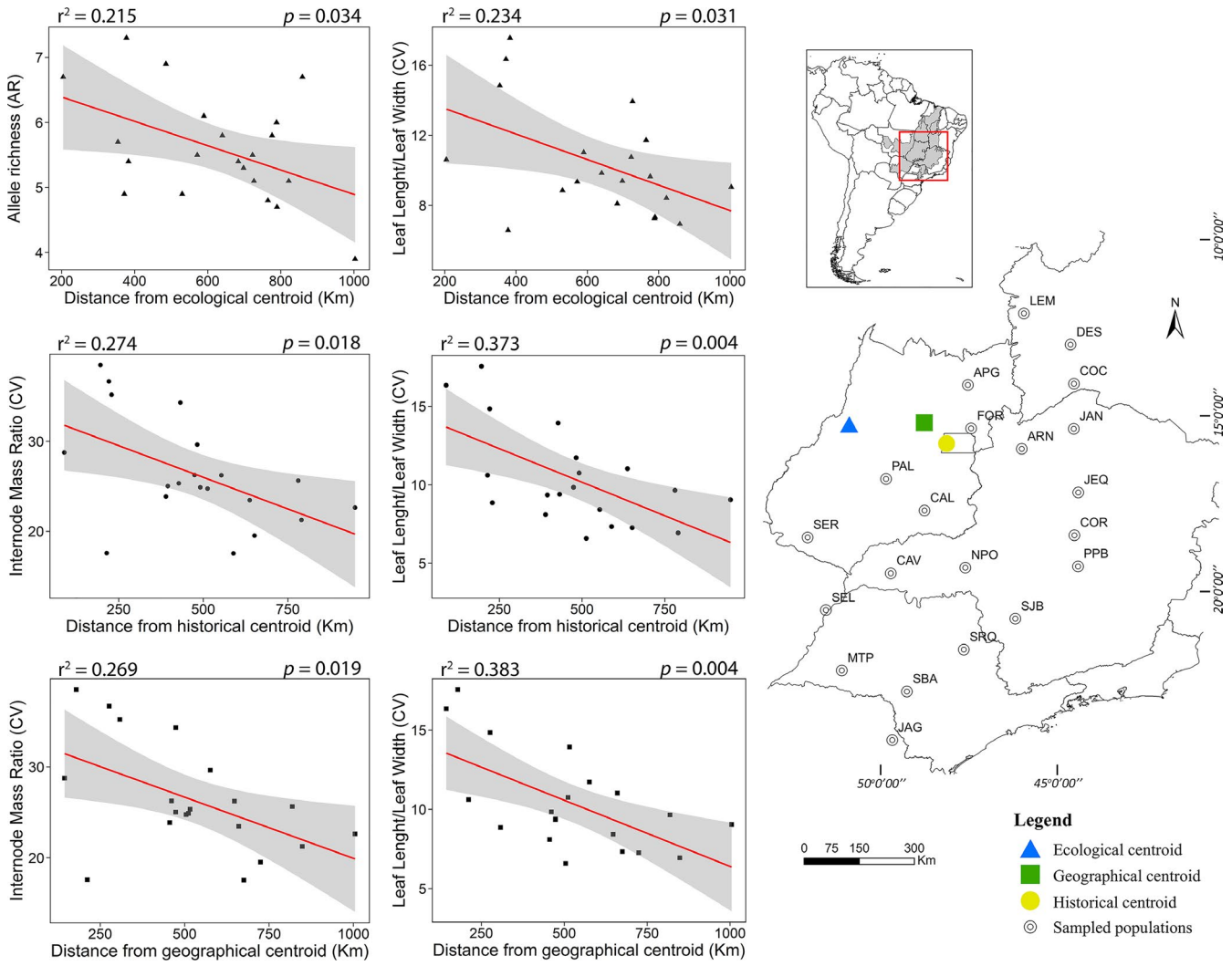

FIGURE 3 Results of significant generalised linear regressions between population genetic and functional trait diversity and population distance from historical, ecological and geographical centres for *Annona crassiflora*. r^2 and *p* values for each linear regression are indicated at the top left and right of each graph, respectively. Symbols on the map represent the estimated location of the ecological (triangle), geographical (square) and historical (circle) centroids for the species and the populations that were sampled for this study (double circle). The grey shade in the South America map represents the Cerrado distribution in Brazil

this area has the highest species richness of Cerrado tree species (Bridgewater et al., 2004; Ratter et al., 2003).

ENM results also suggested the same dynamics of contractions and expansions of *A. crassiflora* distribution range during the late Quaternary as previously observed for *Q. grandiflora* (Buzatti et al., 2018), and for two other *Qualea* species (Buzatti et al., 2017), all endemic and widely distributed in the Cerrado. These contractions and expansions of suitable areas for the species predicted with ENM are concordant with the cycles of expansion and contraction of the Cerrado flora due to the Pleistocene climatic fluctuations. Paleopalinological records have evidenced that during the cooler and drier periods, the Cerrado retracted in its southern portion and expanded east towards the Atlantic Ocean, and north towards the equator (Behling, 1998; Behling & Lichte, 1997).

Besides having the most suitable current area for *A. crassiflora* occurrence, a large climatically stable area (refugium) was predicted to occur in central Cerrado, which is the same area found for other Cerrado tree species (Bueno et al., 2017; Buzatti et al., 2017, 2018; Souza et al., 2017). Phylogeographic studies have revealed high genetic diversity in the central portion of the Cerrado and low diversity in southern Cerrado due to recent colonization (Buzatti et al., 2017, 2018; Collevatti et al., 2003, 2009; Novaes et al., 2010, 2013; Ramos et al., 2007; Souza et al., 2017). In fact, this stable area in central Cerrado is assumed to be an important refugia for the Cerrado biota during Quaternary climatic oscillations (Bueno et al., 2017; Collevatti et al., 2015; Souza et al., 2017; Terribile et al., 2012; Werneck et al., 2012).

The three distinct centroids that were calculated (i.e., ecological, geographical and historical) for each species did not overlap. Divergences between ecological and historical centroids within each species are further evidence that the suitability degree of areas currently occupied by the species changed during the late Quaternary.

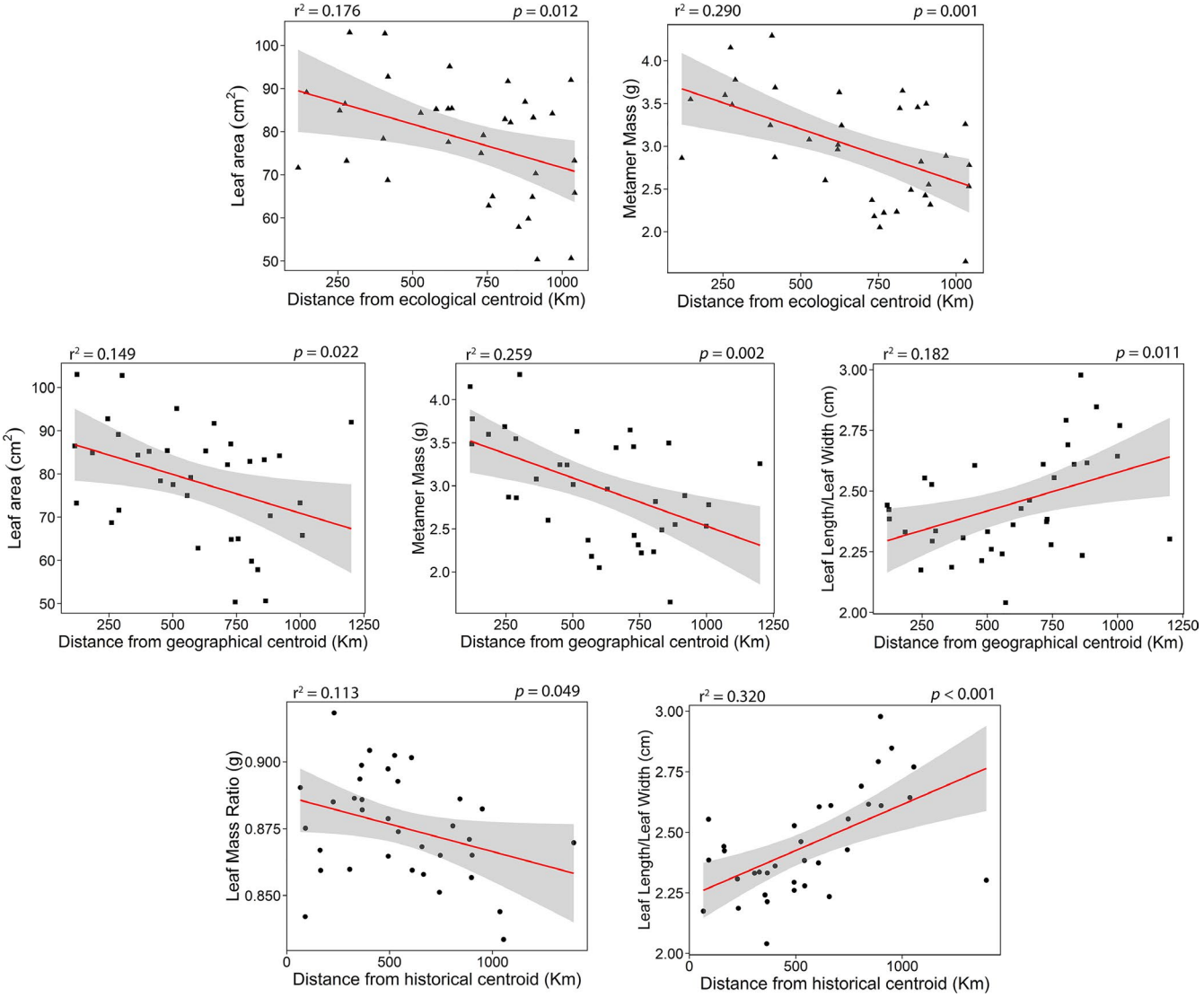

FIGURE 4 Results of significant generalised linear regressions between population leaf trait means and population distances from historical, ecological and geographical centres for *Qualea grandiflora*. r^2 and *p* values for each linear regression are indicated at the top left and right of each graph, respectively

In the same way, differences here observed between the ecological and geographical centres within each species suggest that *Q. grandiflora* and *A. crassiflora* are currently not fully distributed in the most climatically suitable areas.

4.2 | Genetic data and CPH

According to the CPH, we found a negative correlation between A_R and the distance from ecological centre in both *Q. grandiflora and A. crassiflora*. A study testing CPH of another tree species from Cerrado (*Caryocar brasiliense*, Caryocaraceae) found that genetic diversity tends to follow a central-periphery model (Diniz et al., 2009). This species is pollinated by bats, and their seeds are dispersed mainly by gravity (see Collevatti et al., 2003), life history traits that are different from *A. crassiflora* and *Q. grandiflora*. Life history traits play an important role in determining the level and spatial distribution of genetic diversity (Duminil et al., 2007; Hamrick et al., 1993; Lowe et al., 2018). Animal-dispersed species are expected to show lower population differentiation and extensive gene flow, while abiotically dispersed species have stronger genetic structure and differentiation (Duminil et al., 2007; Lowe et al., 2018). These effects of life history traits can either hinder the CPH patterns on the genetic diversity and divergence or increase the marginality effects on populations. Because the same CPH patterns were observed in three phylogenetically distant species, with different life histories in respect to pollination and seed dispersion, we suggest that the premises of the CPH can be strong drivers of genetic diversity across distribution range of Cerrado species, and so other endemic tree species from this biome may also fit the CPH.

Better ecological conditions found in the centre of species distribution range when compared to peripheral areas predicted by

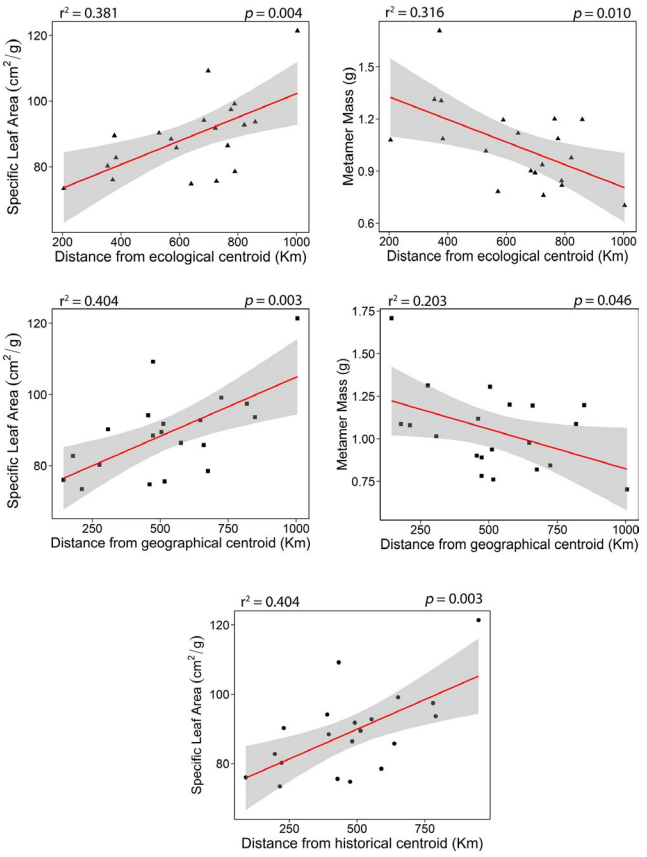

FIGURE 5 Results of significant generalised linear regressions between population leaf trait means and population distances from historical, ecological, and geographical centres for *Annona crassiflora*. r^2 and *p* values for each linear regression are indicated at the top left and right of each graph, respectively

ENM for the *A. crassiflora* (this work) and *Q. grandiflora* (Buzatti et al., 2018) would contribute to the maintenance of larger population sizes and thus higher genetic diversity (Hoffmann & Blows, 1994; Lira-Noriega & Manthey, 2014). The negative relationship between A_R and distance from ecological centres in both species suggests that the lower level of genetic diversity in ecologically peripheral populations might complicate their adaptation to harsher environmental conditions (Blows & Hoffmann, 2005; Pironon et al., 2017; Takahashi et al., 2016). Therefore, these factors may be critical to the survival of these peripheral populations to ongoing climatic changes. The low genetic diversity in marginal populations can also hinder the expansion of these species in non-savannic habitats, which could explain their endemism in the Cerrado. In fact, a study evaluating species endemism in Cerrado concluded that most of its endemism is concentrated in higher elevation central regions of the biome (Vidal et al., 2019). This endemism pattern reinforces the CPH validity for Cerrado species. However, the putative relationship between low genetic diversity of marginal populations and Cerrado species' endemism deserves further investigation through comparisons between several endemic and non-endemic species. The other parameter used to measure genetic diversity, the expected heterozygosity (H_E), showed no centre-periphery patterns for any of the two species investigated. Lower number of associations found between H_E and distances from centres, compared with associations between A_R and distances, was already described in a revision by Eckert et al., (2008). Differences in the number of correlations between H_E and A_R can arise since the estimation of A_R accounts for rare alleles (which are commonly lost during bottlenecks, founder events and fluctuation in population sizes), making A_R more sensible than H_E to stochastic events that commonly occur on species' range edges (Eckert et al., 2008).

The genetic distance among *Q. grandiflora* populations evaluated by F_{ST} index was positively correlated with distances from geographical and historical centres, as expected under CPH. The increase of interpopulation genetic divergence and the decrease of intrapopulation genetic variation towards species' historical range edges are expected under CPH due to historical expansions and contractions at the range edge. Reduction of suitable areas during Quaternary climatic oscillations can result in population extinction or shrinkage in some parts of species distribution and/or cause a reduction in effective population size. This may lead to bottleneck events or local adaptations that can hamper gene flow among populations (Hampe & Petit, 2005; Hewitt, 1996; Wagner et al., 2012) and decrease population genetic diversity. Therefore, higher genetic diversity is expected in populations located at climatically stable areas, like the refuges, compared to the ones located at unstable or historical marginal areas. However, we did not detect a decrease of genetic diversity from the historical centre for both species. Nevertheless, phylogeographical and genetic studies in *Q. grandiflora* and *A. crassiflora* indicated that genetic diversity and structure were shaped by Quaternary climatic changes in both species (Buzatti et al., 2018, 2019; Ribeiro, Souza, et al., (2016). This apparent contradiction between results obtained here and phylogeographical studies indicating effects of past events on genetic diversity, and structure of these species, can be explained by several factors. The no-adjust to CPH, in relation to the historical centre, can indicate that past climatic changes did not lead to a centre-marginal pattern of genetic diversity. Instead, it may have increased the diversity in all populations located within the large central stable areas and small peripheral ones, compared to the ones located outside these refugia. Another probable explanation is the presence of a strong genetic structure shaped by Quaternary climatic fluctuations in both species, with the formation of several genetic groups along the species distribution (Buzatti et al., 2018, 2019; Ribeiro, Souza, et al., 2016), shuffling centre-marginal signs.

4.3 | Functional leaf traits and CPH

Our results bring important insights into the support of CPH in relation to functional leaf traits. In *Q. grandiflora*, only the intrapopulation diversity for MM among the eight evaluated characters was negatively correlated with distances from the historical centre. However, when looking at the mean population values of leaf traits

along the species distribution, we also observe that leaves are overall bigger and the metamers are heavier in populations located at the species geographical and ecological centres. Higher variation of leaf traits in populations that are closer to the historical centre could be expected under the CPH as result of the persistence of more stable and larger populations through the Pleistocene, whereas the small size and instability of peripheral populations would lead to low diversity of these traits. However, considering that neutral genetic diversity did not fit CPH predictions in relation to the historical centre and considering the results obtained for functional traits using population means, it is more likely that the low diversity in MM at the periphery is more a consequence of strong selection pressure under unfavourable environmental conditions, rather than a result of demography.

The heavier MM, greater LA and LMR in central *Q. grandiflora* populations corroborates with a study carried by Abeli et al., (2014). In this study, individual plants growing in central populations were, in general, larger than those growing in peripheral populations, when considering either the whole plant or single organs as measures of plant size. Bigger leaves and heavier metamers point to an outperformance of *Q. grandiflora* populations located in more suitable environmental conditions when compared to populations located in harsher environments. Peripheral populations, besides lower LA and MM, also showed differences in leaf shape when compared to central populations, with higher values of LLW ratio evidencing the effect of harsh conditions in the leaf lamina expansion. According to the CPH, populations located at the ecological marginality would experience a distinct ecological context than those ones located at the species optimum condition resulting in higher mortality due to habitat unsuitability and interspecific competition (Abeli et al., 2014; Herrera & Bazaga, 2008; Hoffmann & Blows, 1994).

The results of *A. crassiflora* leaf traits variation showed consistent centre-periphery patterns with LLW and IMR in peripheral populations exhibiting lower variation in relation to central populations when considering three and two centres, respectively. LLW is an important functional feature related to photosynthetic rates and carbon sequestration capacity (Brodribb et al., 2007). Leaf shapes, here expressed as LLW, have also been linked to the capacity of a plant to adapt to different habitats (Jones et al., 2009) and therefore are expected to vary according to environmental conditions (Buzatti et al., 2019; Jacobs, 1999). In the same way, IMR is related to the hydraulic pathway and biomechanics leaf sheet support (Santiago et al., 2004; Souza et al., 2018). Thereby, according to CPH, besides stochastic factors like genetic drift due to small population sizes (Hampe & Petit, 2005; Lesica & Allendorf, 1995; Meeus et al., 2012), the high selective pressures over functional traits which play vital roles for plant surviving would lead to low phenotypic diversity (Garcia-Ramos & Kirkpatrick, 1997). Similar to *Q. grandiflora*, the mean MM of populations were negatively correlated with distances from geographical and ecological centres in *A. crassiflora*. This common pattern suggests that MM can be a useful trait to discriminate deleterious environmental effects on plant vigour, as observed here in marginal populations of the two studied species. In *A. crassiflora*, the observed increase of SLA towards the periphery seems to contradict the CPH. SLA is a ratio between LA and leaf mass; as MM decreased towards the periphery and the LA remained constant, an increase of SLA is expected in those populations. High SLA is often linked to a high photosynthetic rate and short leaf longevity (Díaz et al., 2004; Walker & Langridge, 2002; Wright et al., 2004) and therefore can be a strategy that favours carbon gain during the growth station, under harsher conditions, on peripheral populations.

It was recently suggested that differentiation among populations for leaf traits in *A. crassiflora* is influenced by differences among climate at the habitat of populations (Ribeiro, Souza, et al., (2016). For *Q. grandiflora*, in addition to climate, soil factors and wind speed were also considered important drivers of leaf trait divergence in populations (Buzatti et al., 2019). Based on these previous studies and considering that optimum environmental factors are expected to be found at the centre of species distribution, we would expect leaf traits to show a centre-periphery pattern of variation. The peculiarities of the adjust of each metamer trait to CPH for both studied species, and the lack of adjust of other studied traits, could be related to the existence of suitable areas with optimum climate and soil conditions for species occurrence along the Cerrado, not only in central areas. Another factor that could have muddled the CPH patterns is the phenotypic plasticity of these traits. In fact, phenotypic plasticity has been suggested to have an important contribution to the phenotypic variation of functional leaf traits in *Q. grandiflora* and other Cerrado tree species (Barros et al., 2012; Goulart et al., 2011; Souza et al., 2018). It has also been demonstrated that phenotypic plasticity is frequently positively associated with heterogeneity of microenvironmental conditions (Barros et al., 2012; Baythavong, 2011; Lázaro-Nogal et al., 2015; Souza et al., 2018), a factor that is not considered in CPH. Thus, study about levels of population phenotypic plasticity along species' range could help better understand the factors that drive the distribution of variation in functional traits. Despite distinct functional leaf traits fitting the CPH differently in the studied species, the results were consistent with a higher plant performance in central when compared to marginal populations.

5 | CONCLUSIONS

Our tests of the CPH for *Q. grandiflora* and *A. crassiflora*, two phylogenetically distant and widely distributed tree species in the Brazilian Cerrado, revealed expected centre-periphery patterns for genetic diversity, when ecological and geographical centres were considered. However, our results showed that genetic structure along the species' range, shaped by past climatic events, can obscure some centre-periphery patterns. Consistent with the CPH prediction of a decrease in environmental suitability towards the periphery, leaf metamer traits exhibited lower vigour from centre to periphery in the two species. Our results highlight the importance

of considering ecological, geographical and historical centres and a great number of populations along species distribution range, to better determine the processes underlying the distribution of neutral genetic diversity, and functional traits. The low genetic diversity and lower leaf metamer vigour in marginal populations can hinder the expansion of the studied species in non-savannic habitats, which may contribute towards explaining their endemism in the Cerrado. Evaluating the centre-periphery patterns of genetic and functional traits diversity increases our knowledge about the factors that shape the current genetic and functional diversity of these species. Furthermore, it is fundamental in predicting the species' capacity to face environmental changes, and in identifying critical areas for their protection, especially considering ongoing climatic changes. For the two studied species, lower genetic diversity and leaf metamer vigour in peripheral populations suggest a low potential for adaptation to the new climatic conditions in these populations.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in two distinct repositories. Microsatellite genotypes and morphological data of *Annona crassiflora* are available in Dryad at https://doi.org/10.5061/dryad.n7dv6. Microsatellite genotypes and morphological data of *Qualea grandiflora* are available in Figshare at https://doi.org/10.6084/m9.figshare.11106881.v2.

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BIOSKETCH

The authors are interested in the evolutionary history and biogeography of Neotropical plants. The authors bring different expertise, forming a complementary team that spans from sampling and data collection to hypothesis generation and testing about genetic and functional diversity of populations of Neotropical species.

Author contributions: MBL, JPL-F, TRP and RSOB designed the study; JPL-F and MBL collected samples; TRP and RSOB generated morphological and genetic data; MLB performed ecological niche modelling; TRP and ACM performed data analysis; TRP, JPL-F and MBL wrote the paper and all authors contributed with comments.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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